

AGRONOMIC MODELING

Modeling Elevated Carbon Dioxide Effects on Water Relations, Water Use, and Growth of Irrigated Sorghum

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ABSTRACT

Elevated concentrations of atmospheric CO₂ (C_a) are believed to raise sorghum [*Sorghum bicolor* (L.) Moench] productivity by improving water relations. In *ecosys*, water relations are simulated by solving for the canopy water potential (ψ_c) at which water uptake from a model of soil-root-canopy water transfer equilibrates with transpiration from the canopy energy balance. Simulated water relations were tested with ψ_c , water uptake, and energy exchange measured under ambient (363 $\mu\text{mol mol}^{-1}$) and elevated (566 $\mu\text{mol mol}^{-1}$) C_a and high vs. low irrigation in a free air CO₂ enrichment experiment during 1998 and 1999. Model results, corroborated by field measurements, showed that elevated C_a raised ψ_c and lowered latent heat fluxes under high irrigation and delayed water stress under low irrigation. Changes in ψ_c modeled under ambient vs. elevated C_a varied diurnally, with lower ψ_c causing earlier midafternoon stomatal closure under ambient C_a. Modeled changes in sorghum water status caused elevated C_a to raise seasonal water efficiency under high and low irrigation by 20 and 26% (vs. 20 and 13% measured) in 1998 and by 9 and 27% (vs. 6 and 26% measured) in 1999. *Ecosys* was used to generate an irrigation response function for sorghum yield, which indicated that yields would rise by $\approx 13\%$ for a range of irrigation rates if air temperatures were to rise by 3°C and C_a by 50%. Current high sorghum yields could be achieved with ≈ 120 mm or $\approx 20\%$ less irrigation water if these rises in temperature and C_a were to occur.

RISE IN CONCENTRATIONS of C_a and other greenhouse gases are believed to be causing changes in climate that may have important impacts on water use in food production. These impacts will result from several contrasting effects of climate change on terrestrial water use. The most direct impact is the reduction in transpiration caused by lower stomatal conductance (g_c) commonly found under elevated C_a. In several FACE experiments with ample water and N, Kimball et al. (2002) reported that a 190 $\mu\text{mol mol}^{-1}$ rise in C_a reduced g_c 's measured in sorghum, wheat (*Triticum aestivum* L.), and cotton (*Gossypium hirsutum* L.) by ≈ 37 , 34, and

15%, respectively. These reductions may be larger under N limitation (Wall et al., 2001a).

However, the effect of lower g_c on transpiration under elevated C_a may be partially offset by a rise in canopy temperature (T_c) and hence canopy vapor pressure (Kimball et al., 1999). This effect may also be offset by an increase in leaf area and hence radiative loading (Kimball et al., 2002). In FACE experiments with ample water and N, Kimball et al. (2002) reported that a 190 $\mu\text{mol mol}^{-1}$ rise in C_a raised temperatures and leaf area index of C₃ grasses by 0.6°C and 11%, respectively.

Another direct impact of climate change on water use is the increase in transpiration caused by larger canopy-atmosphere vapor pressure gradients that develop under rising air temperatures. The increase in these gradients is believed to be only partially offset by rising atmospheric humidity caused by more rapid evapotranspiration. Thus, regional soil drying is a projected consequence of some climate change scenarios unless accompanied by substantial increases in precipitation. On the other hand, rising air temperatures also hasten crop development and hence shorten growing seasons, reducing water use. There is much uncertainty about the net effects of elevated C_a and temperature on crop water requirements.

Ecosystem models have frequently been used to account for these contrasting impacts of climate change on terrestrial water use. Hatch et al. (1999) used the CROPGRO (e.g., Jones et al., 1988) and CERES (Jones and Kiniry, 1986) models to predict reductions of up to 50% in the irrigation requirements of field crops after 100 yr of climate change simulated by the U.K. Meteorological Office (UKMO) general circulation model (GCM) in the southeast USA. These reductions were attributed to higher C_a and precipitation and to shortened growing seasons caused by more rapid phenological advance under higher temperatures. Strzepek et al. (1999) used the same crop models to predict reductions of up to 20% in the irrigation requirements of maize (*Zea mays* L.) after 50 yr of Goddard Institute of Space Studies (GISS) and Geophysical Fluid Dynamics Laboratory (GFDL)

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Abbreviations: C_a, atmospheric CO₂; C_i, intercellular CO₂ concentration; DOY, day of year; FACE, free air CO₂ enrichment (experiment); g_c , stomatal conductance; GCM, general circulation model; g_L , leaf conductance; H , sensible heat; IRTs, infrared thermometers; LE, latent heat; R_n, net radiation; T_c , canopy temperature; VPD, vapor pressure deficit; WUE, water use efficiency; ψ_c , canopy water potential; ψ_s , soil water potential; ψ_T , canopy turgor potential; ψ_π , osmotic potential; Ω_R , root-canopy hydraulic resistances; Ω_s , soil-root hydraulic resistances.

GCM climate change in the midwestern USA. These reductions were also attributed to shortened growing seasons caused by higher temperatures. In the same study, Strzepek et al. (1999) predicted increases of up to 75% in the irrigation requirements of soybean [*Glycine max* (L.) Merr.]. These increases were attributed to longer growing seasons caused by the photoperiod response of soybean to earlier planting. Tubiello et al. (2000) used CropSyst (Stockle et al., 1994) to predict that shortened growing seasons would reduce irrigation requirements by 60% for maize, 50% for soybean, and 10% for sorghum in Italy after 100 yr of GISS and GFDL GCM climate change. However, they found that increases in irrigation of 60 to 90% for maize and soybean and of 15% for sorghum would be required to maintain current yields under these climate change scenarios.

The effects of elevated C_a on crop water requirements have been modeled on a daily time step by altering the Priestley–Taylor (Strzepek et al., 1999) or Penman–Monteith (Tubiello et al., 2000) equations to account for decreased g_c under elevated C_a . Crop water use in these models may be constrained by soil water uptake calculated daily from soil–canopy water potential gradients and empirically estimated root distributions (Jara and Stockle, 1999). However, these modeling techniques require the temporal averaging of diurnally varying phenomena such as ψ_c and g_c , which respond very nonlinearly to diurnal changes in weather. Important effects of elevated C_a on transpiration caused by higher T_c 's (Kimball et al., 1999) and water potentials (Wall et al., 2001b) cannot be simulated with these techniques. These modeling techniques can only be tested with temporally aggregated field data (e.g., seasonal phytomass or evapotranspiration) that cannot distinguish among alternative process-level hypotheses. The effects of elevated C_a on transpiration would in theory be better modeled at time scales more consistent with that at which these effects occur (e.g., hourly).

It is important that model results be subjected to well-constrained tests before models are used in predictive studies of climate change effects. Generally speaking, model tests become better constrained as their spatial and temporal resolutions increase. The use of energy fluxes in model testing is well constrained in that test data are highly resolved temporally and flux theory is comparatively well defined. Atmospheric CO_2 effects on crop water requirements are therefore best modeled by explicitly simulating the diurnal changes in ecosystem–atmosphere energy exchange by which evapotranspiration is driven. This modeling requires the coupling of closure schemes for canopy and soil surface energy balances with transfer schemes for soil water movement and root water uptake. This coupling must occur at a time scale that allows the large diurnal variation in these energy balances to be represented. In earlier work, we tested algorithms for coupling energy balances with water uptake in *ecosys* (<http://www.rr2.ualberta.ca/Research/ecosys/>; verified 26 Aug. 2004) (Grant, 2001) with findings from a FACE experiment on wheat (Grant et al., 1995a, 1995b, 1999). We now extend this testing to sor-

ghum to determine whether these same algorithms can simulate C_a effects on water use by a C_4 crop grown under much higher temperatures. We then use these algorithms to estimate climate change effects on irrigation requirements of sorghum.

MODEL DEVELOPMENT

Energy Exchange

Energy exchanges between the atmosphere and terrestrial surfaces are resolved in *ecosys* into those between the atmosphere and the leaf and stem surfaces of each population (e.g., species or cohort) within the plant community and those between the atmosphere and each of the surfaces (soil, plant residue, and snow) of the ground beneath (Grant et al., 1999). Total energy exchange between the atmosphere and terrestrial surfaces is calculated as the sum of exchanges with all plant and ground surfaces. Surface energy exchange is coupled with soil heat and water transfers, including runoff (Manning), infiltration (Green-Ampt), macropore flow (Poiseuille), and micropore flow (Richards).

Canopy energy exchange in *ecosys* is calculated from an hourly two-stage convergence solution for the transfer of water and heat through a multilayered multipopulation soil–root–canopy system. The first stage of this solution requires convergence to a value of T_c for each plant population at which the first-order closure of the canopy energy balance (net radiation, sensible heat flux, latent heat flux, and change in heat storage) is achieved (Eq. 1–15 in Grant et al., 1999). These fluxes are controlled by aerodynamic conductance (g_a) and g_c . Two controlling mechanisms are postulated for g_c :

1. At the leaf level, a maximum leaf conductance (g_L) is calculated for each leaf surface that allows an initial intercellular CO_2 concentration (C_i)/ C_a ratio for sorghum of 0.45 (Williams et al., 2001) to be maintained at carboxylation rates calculated under ambient irradiance, temperature, C_a , and full turgor. This ratio will be allowed to vary diurnally when hourly canopy water status is solved at a later stage in the calculations as described in the Carbon Dioxide Fixation section below. The modeling of carboxylation rates has been elaborated from earlier work to include C_4 processes. In C_4 plants, the mesophyll carboxylation rate is the lesser of CO_2 - and light-limited reaction rates (Berry and Farquhar, 1977). The CO_2 -limited rate is a Michaelis–Menten function of PEP carboxylase activity and aqueous CO_2 concentration in the mesophyll parameterized from Berry and Farquhar (1977) and from Edwards and Walker (1983). The light-limited rate is a hyperbolic function of absorbed irradiance and mesophyll chlorophyll activity with a quantum requirement from Berry and Farquhar (1977). The mesophyll concentration of the C_4 carboxylation product drives a mesophyll-bundle sheath transfer algorithm that maintains a set bundle sheath/mesophyll C_4 concentration ratio. The bundle sheath concentration drives a decarboxylation re-

action, the CO₂ product of which drives a C₃ carboxylation model (Farquhar et al., 1980) in the bundle sheath parameterized for C₄ plants from Seeman et al. (1984) and a leakiness algorithm that returns CO₂ from the bundle sheath to the mesophyll. Carboxylase and chlorophyll activities in both the mesophyll and bundle sheath are the products of specific activities and concentrations. Specific activities are constrained by C₄ and C₃ (Bowes, 1991; Stitt, 1991) product inhibition so that both mesophyll and bundle sheath carboxylation rates are fully coupled to rates of product removal. Product removal rates are determined by phyto-mass biosynthesis rates that are controlled by plant water and nutrient status. Carboxylase and chlorophyll concentrations in both the mesophyll and bundle sheath are set from leaf structural N concentrations. These concentrations are determined by leaf nonstructural N/C ratios controlled by plant nutrient status. This C₄ carboxylation model gives bundle sheath CO₂ concentrations similar to those reported by Furbank and Hatch (1987) and bundle sheath CO₂ leakiness, expressed as a fraction of PEP carboxylation, similar to that measured by Williams et al. (2001). Leaf carboxylation rates from this model are then used with the initial C_i/C_a to calculate maximum g_L , which is then aggregated by leaf surface area to maximum g_C for use in the energy balance convergence scheme (Grant et al., 1999).

- At the canopy level, g_C is then reduced from that at full turgor through an exponential function of canopy turgor potential (ψ_T) determined from total ψ_C and osmotic potential (ψ_π) generated during convergence for transpiration vs. water uptake. The calculation of ψ_C is described in the Water Relations section below. The exponential function of ψ_T used here is based on that proposed by Zur and Jones (1981) to account for the effects of osmotic adjustment on g_C . There is no direct response of g_C to vapor pressure deficit (VPD) in *ecosys* although such a response is included in most other models of g_C . However, larger VPD raises transpiration, forcing lower ψ_C and ψ_T to be calculated in *ecosys* during convergence for transpiration vs. water uptake. The exponential function used to calculate g_C from ψ_T causes g_C to become more sensitive to ψ_T as ψ_C and ψ_T decline. In wet soil, ψ_C and ψ_T may be high enough that g_C is not very sensitive to VPD, as has been found experimentally by Garcia et al. (1998). However, g_C becomes more sensitive to VPD as soil or atmospheric water deficits become more severe.

Water Relations

After convergence for T_C is achieved, the difference between canopy transpiration E from the energy balance and total water uptake U from all rooted layers in the soil is tested against the difference between canopy water content from the previous hour and that from

the current hour (Grant et al., 1999). This difference is minimized by adjusting ψ_C , which determines each term from which this difference is calculated. The value of ψ_C determines that of ψ_T , and hence of g_C , through its effect on ψ_π (Girma and Krieg, 1991; Grant, 1995; Eq. 24–25 in Grant et al., 1999). The difference between ψ_C and soil water potential (ψ_s) determines U by establishing potential differences across soil–root (Ω_s) and root–canopy (Ω_R) hydraulic resistances and in each rooted soil layer (Eq. 32–37 in Grant et al., 1999). Hydraulic resistances are calculated from Poiseuille's law using root radial and axial resistivities derived by Doussan et al. (1998) with root lengths and surface areas from a root system submodel (Grant, 1998). Changes in ψ_C determine those in canopy water content according to plant water potential–water content relationships (e.g., Acevedo et al., 1979; Saliendra and Meizner, 1991). Because g_C and T_C both drive E , the canopy energy balance described under the Energy Exchange section above is recalculated for each adjusted value of ψ_C during convergence.

Carbon Dioxide Fixation

After successful convergence for T_C and ψ_C , leaf carboxylation rates are adjusted from those calculated under full ψ_T to those under ambient ψ_T . This adjustment is required by the decrease in g_C from its maximum value (calculated in the Energy Exchange section above) to that at ambient ψ_T (calculated in the Water Relations section above). The adjustment is achieved through a convergence solution for C_i at which the diffusion rate of gaseous CO₂ between C_a and C_i through g_L (Eq. 48–53 in Grant et al., 1999) equals the carboxylation rate of aqueous CO₂ at the aqueous equivalent of C_i (described in the Energy Exchange section above). This convergence arrives at a lower C_i than that at full ψ_T so that C_i/C_a declines under water stress as found by Williams et al. (2001). The CO₂ fixation rate of each leaf surface at convergence is added to arrive at a value for gross canopy CO₂ fixation by each tiller (or branch) of each plant population (i.e., species or cohort) in the model.

Carbon Respiration

The product of CO₂ fixation is added to a nonstructural C pool from which C is oxidized (Eq. 26–31 in Grant et al., 1999). Oxidized C is first used to meet requirements for maintenance respiration, and then any excess is used to drive biosynthesis according to organ-specific growth yields. Low nonstructural C may cause C oxidation to be less than maintenance requirements, in which case the shortfall is made up through respiration of remobilizable protein C withdrawn from lamina and sheath C. Upon exhaustion of the remobilizable protein C in each lamina or sheath, the remaining structural C is dropped from the tiller and added to the soil surface as litter. Environmental constraints such as nutrient, heat, or water stress that reduce nonstructural C formation and hence oxidation with respect to maintenance requirements will therefore hasten the loss of lamina and sheath C from the plant. Net canopy CO₂ fixation

is calculated as the difference between aggregated leaf carboxylation rates and C oxidation rates.

FIELD EXPERIMENT

Crop Management

A 12-ha laser-leveled field of Trix clay loam [fine-loamy mixed (calcareous) hyperthermic Typic Torrifluvent] at the University of Arizona's Maricopa Agricultural Research Center (MAC) 30 km south of Phoenix, AZ, was fertilized and cultivated on 10 June 1998 and 1 June 1999 (Table 1). Sorghum (DeKalb hybrid 'DK54') was planted on 15–16 July 1998 and 15–16 June 1999 in 0.76-m rows to give populations of 22 plants m^{-2} (1998) and 26 plants m^{-2} (1999). Research plots in the "wet" treatment were flood-irrigated from adjacent canals to replace evapotranspirational demand whenever $\approx 30\%$ of plant available water in the rooted soil zone was depleted (Table 1). Plots in the "dry" treatment received fewer irrigations. Additional fertilizer was added in irrigation water (Table 1). The field was located within an irrigated area that extended for more than 1 km in all directions so that most of the area surrounding the site was irrigated during the entire experiment. Some damage to the sorghum was caused by frosts after 10 Nov. 1998 and by hail on 16 Sept. 1999. Plots were harvested on 21 Dec. 1998 and 26 Oct. 1999. Further details about crop management are given in Ottman et al. (2001).

Hourly averages of solar radiation, air temperature, wind speed and humidity, and hourly totals of precipitation were recorded at a height of 2 m over the field site and at the Arizona Meteorological Network (AZMET) station on the Maricopa Research Center about 1 km away. Soil water contents were measured before and after each irrigation in all plots using a neutron probe

(Hydroprobe Model 503 CR, Campbell Pacific Co., Martinez, CA) at 0.3-m increments from 0.46 to 1.8 m (1998) or from 0.23 to 3.0 m (1999). Evapotranspiration was calculated for each plot as irrigation + rainfall – change in soil water content within the estimated rooting zone during both growing seasons (Conley et al., 2001). A pressure chamber (Model 3000, Soil Moisture Equipment Corp., Santa Barbara, CA) was used to measure midday water potentials in the midribs of blades excised from uppermost fully expanded leaves (Wall et al., 2001b). Dry masses of different plant components (leaves, crowns, stems, chaff, and grain) were measured weekly from eight plants in each replicate of each treatment (Ottman et al., 2001). Leaf area was measured weekly on the sampled plants using a leaf area machine (LI-3100, LI-COR, Lincoln, NE).

Carbon Dioxide Treatments

Four replicates of control and FACE treatments (Hendrey, 1993), consisting of toroidal plenum rings constructed from 30-cm-diam. pipe with 2.5-m vertical pipes located every 2.4 m around the periphery, were established in 25-m-diam. circular plots shortly after seeding. These rings were mounted on 15-cm blocks to avoid interfering with the flood irrigation and located such that one-half of each ring was in each of the wet and dry irrigation treatments. From 31 July to 8 December 1998 and from 2 July to 19 October 1999 (50% emergence to maturity), a computer control system used wind speed, wind direction, and CO_2 concentration measured at the center of each control vs. FACE ring to regulate CO_2 emission from vertical pipes upwind of the plots. During emission, ambient air (control) or CO_2 -enriched air (FACE) was released upwind of the plots through holes in the vertical pipes at elevations from 0.5 to 2.0 m, depending on crop height. Average daytime CO_2 concentration maintained over the FACE plots was $556 \mu mol mol^{-1}$ in 1998 and $566 \mu mol mol^{-1}$ in 1999 while those over the control plots were $363 \mu mol mol^{-1}$ in 1998 and $373 \mu mol mol^{-1}$ in 1999. One-minute-averaged CO_2 concentrations measured in the plots were within 10% of these values 87% of the time. Further details about CO_2 treatments are given in Ottman et al. (2001).

Energy Exchange Measurements

The plots were semicircular with a useable radius of only about 10 m, providing limited fetch for calculating $CO_2 \times$ irrigation effects on evapotranspiration from profiles of wind speed, temperature, and water vapor measured above the crop. Therefore, a residual energy balance method was used to calculate latent heat fluxes from the individual plots (e.g., Huband and Monteith, 1986). This technique was reasoned to be less sensitive to fetch constraints because:

1. All plots were in a field of sorghum in which all structural elements were close to the same size and geometry. Therefore, aerodynamic resistance would not be expected to vary much among plots.

Table 1. Dates and amounts of irrigation and fertilization in the wet and dry treatments during 1998–1999.

Date	Irrigation		Fertilizer	
	Wet	Dry	Wet	Dry
	mm		$g m^{-2}$ or $mg L^{-1} \dagger$	
1998				
10 June			9.3	9.3
28 July	281	281		
14 August	352			
28 August	154			
11 September	120	195	103.3	95.4
25 September	120		51.7	
8 October	120			
22 October	108			
Rainfall‡	35	35		
Total	1290	511	27.9	27.9
1999				
1 June			9.3	9.3
28 June	153	153		
23 July	161			
6 August	185	185	93.0	93.0
20 August	138			
3 September	129			
Rainfall	152	152		
Total	918	490	26.5	26.5

† Dryland applications as urea and incorporated by harrow on 10 June 1998 and 1 June 1999 are given in $g m^{-2}$; applications in water as urea ammonium nitrate during irrigation events on the same dates are given in $mg L^{-1}$. Total fertilizer applications are in $g m^{-2}$.

‡ After 1 May 1998.

2. Turbulent transfer processes are a logarithmic function of height above the crop surface so that gradients close to the crop are largest and most important in determining rates of heat transfer. Crop surface temperatures were measured with infrared thermometers (IRTs) that were not affected by wind speed, thereby minimizing fetch requirements. The parameters for canopy emittance and reflected sky radiation used in the calculation of surface temperatures for this study were found by Huband and Monteith (1986) to give unbiased differences between radiative and aerodynamic temperatures of not >1.5 K and usually <1 K. Under the conditions of the FACE experiment, a difference of 1 K between radiative and aerodynamic temperatures would cause a difference of as much as 60 W m^{-2} in the calculation of sensible heat flux. However, this difference would not be systematic.

During most of the experiment, net radiation (R_n) was measured every 15 min using net radiometers (Model Q6, Radiation and Energy Balance Syst. Inc., Seattle, WA) calibrated before and after the experiment against a standard net radiometer (Model LXV 055, DR Lange, Germany). The net radiometers were mounted 1.0 m above the crop in two replicates of each C_a and irrigation treatment where they were raised, cleaned, and leveled weekly. Soil heat flux was measured from four soil heat flux plates (Model HFT-3, Radiation Energy Balance Syst., Seattle, WA) placed at a depth of 10 mm between sorghum rows in two replicates of each $C_a \times$ irrigation treatment. A thermocouple was placed at a depth of 5 mm above each heat flux plate to measure changes in soil heat storage. Sensible heat flux was calculated from T_c 's measured with stationary IRTs (Model 4000a, 15° field of view, Everest Interscience, Tustin, CA) calibrated against an extended-area black-body source (Model EABB-250, Advanced Kinetics, Huntington Beach, CA) and from dry and wet bulb temperatures measured with a pair of aspirated psychrometers. The IRTs were positioned 1 m above the sorghum in two replicates of each $C_a \times$ irrigation treatment to view the crop canopy northward at a zenith angle of 45°. Infrared thermometer temperatures were corrected for canopy emittance and reflected sky radiation to account for differences between radiative and aerodynamic surface temperatures (Huband and Monteith, 1986). The aspirated psychrometers were mounted at a height of 2 m in the same plots as the net radiometers. Aerodynamic resistances used in sensible heat flux calculations were computed from wind speed measured at 2 m above the ground with a three-cup anemometer and photochopper (Model 12102D, R.M. Young Co., Traverse City, MI) and from zero plane displacement and roughness length calculated from canopy height (Azevedo and Verma, 1986), using a nonisothermal stability correction (Mahrt and Ek, 1984). Further details about the energy exchange measurements are given in Triggs et al. (2004).

SIMULATION EXPERIMENT

The simulation model *ecosys* was initialized with the physical and chemical properties of Trix clay loam (Table 1 in Grant et al., 1999) and the biological properties of sorghum derived from literature sources [including kinetic constants and concentrations of carboxylases and chlorophyll for C_3 and C_4 reactions (Berry and Farquhar, 1977; Ku et al., 1979; Seeman et al., 1984), C_i/C_a ratio (Williams et al., 2001), leaf optical properties, canopy and root architecture parameters (Aguirrezabal et al., 1993; Klepper, 1990), kinetic constants for root nutrient uptake (Barber and Cushman, 1981), and parameters for root (Reid and Huck, 1990; Doussan et al., 1998) and stomatal (Girma and Krieg, 1992) conductances]. The model was run from 1 May 1998 to 31 Oct. 1999 at $C_a = 363$ or $556 \mu\text{mol mol}^{-1}$ (1998) and at $C_a = 373$ or $566 \mu\text{mol mol}^{-1}$ (1999) under the irrigation and fertilization schedules for the wet and dry treatments (Table 1) using management practices and hourly meteorological data reported from the field site. Because some of the flood irrigation was observed to flow through soil cracks, soil macroporosity was set in the model to approximate the loss of irrigation water inferred from neutron probe readings taken immediately before and after each irrigation. Initial soil water, NH_4^+ , and NO_3^- contents were selected to give those measured on 23 July 1998 in each soil horizon of each treatment. All site-specific inputs required by *ecosys* were confined to site, soil, and plant properties that could be measured independently of the model. All model parameters for CO_2 fixation (except PEP carboxylation), respiration, and partitioning by plant and microbial populations were the same as those used in earlier studies of C and energy exchange over agricultural crops (Grant and Baldocchi, 1992; Grant et al., 1993, 1995a, 1995b, 1999).

Hourly totals of canopy + ground R_n (Eq. [2] and [17] in Grant et al., 1999), latent heat (LE) (Eq. [3] and [18] in Grant et al., 1999), and sensible heat (H) (Eq. [5] and [19] in Grant et al., 1999) simulated in *ecosys* were compared with hourly averaged R_n , LE, and H measured under 363 vs. $556 \mu\text{mol mol}^{-1}$ C_a (1998) or 373 vs. $566 \mu\text{mol mol}^{-1}$ C_a (1999) in the wet and dry treatments. Accumulated evapotranspiration simulated by *ecosys* from LE in each $C_a \times$ irrigation treatment was compared with that estimated from neutron probe measurements during both growing seasons. Phytomass simulated for each $C_a \times$ irrigation treatment was compared with weekly measurements.

A relationship between irrigation amount and sorghum yield was then derived by running *ecosys* from 1 May to 31 Oct. 1999 using 1999 meteorological data and crop management with a range of irrigation rates applied in a biweekly schedule. Initial conditions for these runs were those simulated on 30 Apr. 1999 by the 1998–1999 *ecosys* model run under ambient C_a and high irrigation (Table 1). The relationship was then derived under hypothesized rises of 3.0°C in 1999 air temperatures and of 50% in ambient C_a to establish its sensitivity to likely changes in future climate.

RESULTS

Diurnal Energy Exchange under Ambient vs. Elevated Atmospheric Carbon Dioxide

In the model, elevated C_a caused only small increases in leaf carboxylation rates because aqueous CO_2 concentrations maintained in the bundle sheath (1–2 mM depending on rates of C_4 production in the mesophyll) were much larger than the Michaelis–Menten constant (K_m) for C_3 carboxylation (30 μM at 25°C). However, elevated C_a caused an increase in the C_a – C_i gradient that was proportional to that in C_a because C_i/C_a ratios in the model were conserved although not constant. Dividing the carboxylation rate by the C_a – C_i gradient therefore gave smaller values when calculating maximum g_L under elevated vs. ambient C_a . When scaled to the canopy level, smaller g_C reduced LE simulated under elevated C_a from that under ambient C_a . This effect of g_C on LE was partially offset by that of a rise in vapor pressure gradient caused by a rise in T_C modeled from the first-order closure of the canopy energy balance under elevated vs. ambient C_a .

The net effects of g_C and T_C on LE under elevated vs. ambient C_a are shown from day of year (DOY) 247 to 251 (4 to 9 September) 1999, immediately after irrigation on DOY 246 (Table 1), during the second year of the model run (Fig. 1). In the wet treatment, high ψ_s and low Ω_s and Ω_R allowed ψ_C and ψ_T in the model to be maintained at values high enough that g_C did not decline, even under high VPD. High g_C allowed rapid effluxes of LE (up to 700 W m^{-2} in Fig. 1a), even though midafternoon VPD reached 5 kPa, indicating that g_C was correctly modeled not to be sensitive to VPD when ψ_s was high. Elevated C_a reduced both simulated and measured LE and increased simulated and measured H by 0 to 50 W m^{-2} (Fig. 1b vs. 1a). In the dry treatment, lower ψ_s and higher Ω_s and Ω_R forced ψ_C and ψ_T in the model to decline under higher VPD to values that caused g_C to decline, reducing LE (midday values declined from 250 W m^{-2} to 150 W m^{-2} during this period with soil drying in Fig. 1c). Thus, g_C was correctly modeled to be more sensitive to VPD when ψ_s was low. Elevated C_a caused lower LE to be simulated earlier in the season, slowing soil water depletion and

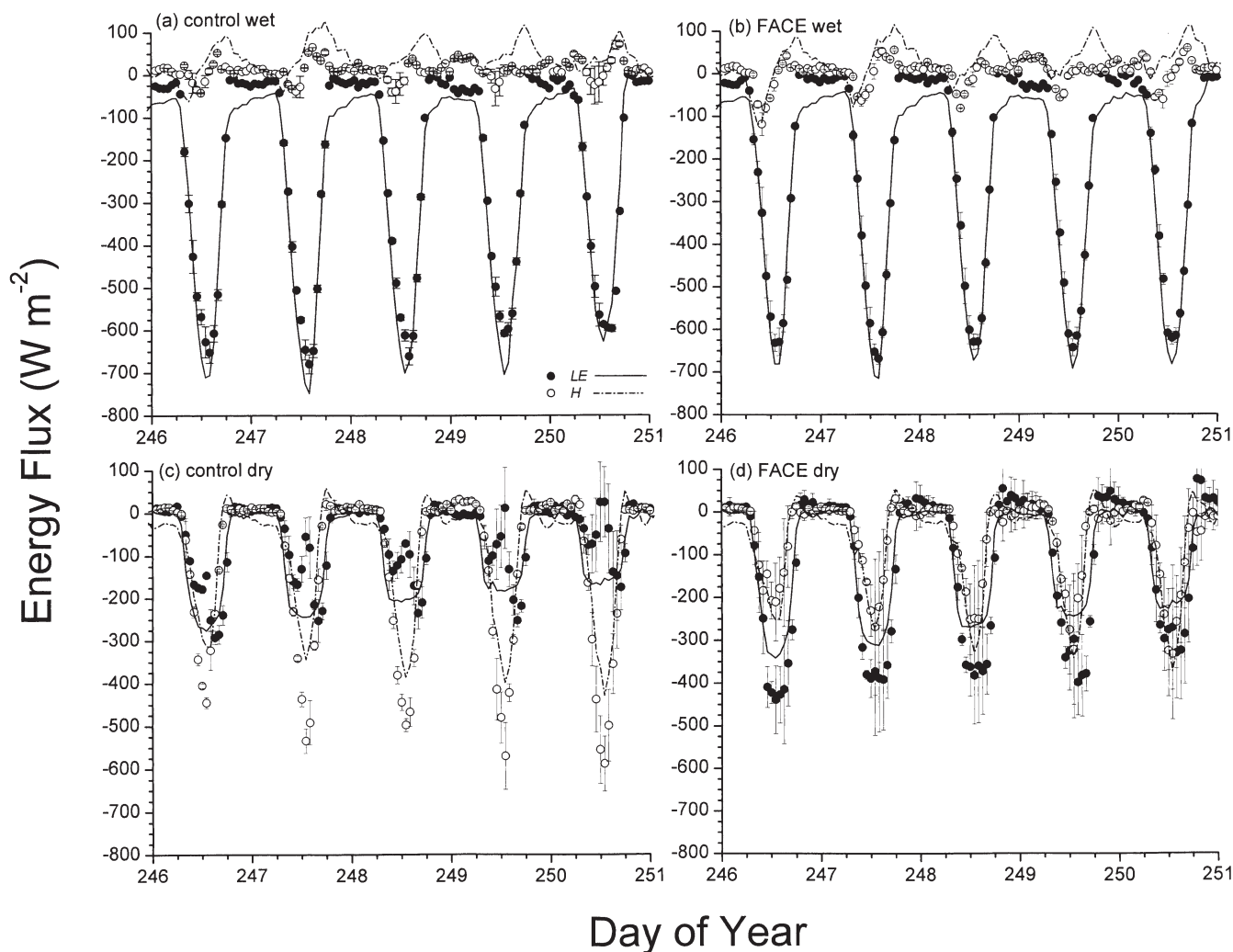


Fig. 1. Net radiation, latent heat (LE), and sensible heat (H) fluxes simulated (lines) and measured (symbols) over sorghum during day of year 247 to 251 (4–8 September) 1999 in the (a) control wet, (b) free air CO_2 enrichment (FACE) wet, (c) control dry, and (d) FACE dry treatments. Downward fluxes (influxes) are positive, and upward fluxes (effluxes) are negative. For irrigation schedules, see Table 1.

delaying the onset of water stress. During DOY 247 to 251, higher ψ_s simulated under elevated C_a allowed sorghum to maintain higher ψ_c and ψ_T , and hence higher g_c , so that simulated and measured LE were raised and H lowered by 50 to 100 W m⁻² from those under ambient C_a (Fig. 1d vs. 1c). Higher ψ_T and g_c under elevated C_a in the dry treatment caused midday Bowen ratios in both the model and the field to be reduced from >1 under ambient C_a to <1 under elevated C_a during early September 1999.

Regressions of modeled on measured LE during 1998 and 1999 indicated that differences between modeled and measured fluxes were comparable to replicate differences in the measured fluxes for all four $C_a \times$ irrigation treatments (Table 2). Regression parameters indicated close agreement between modeled and measured LE in the wet treatments of both years ($b > 0.9$, $R^2 > 0.8$) and in the dry treatment of 1998 but lower modeled vs. measured LE in the dry treatment of 1999 ($b < 0.8$, $R^2 < 0.8$).

Water Relations under Ambient vs. Elevated Atmospheric Carbon Dioxide

Lower g_c and hence lower LE allowed higher ψ_s and smaller soil-root-canopy ψ gradients to be simulated during convergence for canopy transpiration vs. root water uptake under elevated vs. ambient C_a . These changes allowed higher ψ_c to be maintained in the model under elevated vs. ambient C_a as was found in the field plots (Fig. 2). During the measurement periods in 1998 and 1999, the average simulated (vs. measured) rises in midday ψ_c were 0.17 MPa (vs. 0.04 ± 0.06 MPa) in the wet treatment and 0.21 MPa (vs. 0.16 ± 0.06 MPa) in the dry treatment (measured values from Wall et al., 2001b). Simulated and measured ψ_c were usually within 0.5 MPa, except after late September 1998 when simulated values rose above -1 MPa while measured values declined below -1 MPa. During this period, rising ψ_c was modeled in response to declining LE that was simulated under declining radiation and temperature. Both modeled and measured midday LE effluxes declined

from >500 W m⁻² in late September 1998 to <400 W m⁻² in mid-October 1998 and <300 W m⁻² in late October 1998, allowing modeled ψ_c to rise.

Elevated C_a raised modeled CO₂ fixation rates directly by raising aqueous CO₂ concentrations in the mesophyll and hence the bundle sheath (although this effect was small as described earlier). Elevated C_a raised modeled CO₂ fixation rates indirectly by lowering g_c and hence transpiration (Fig. 1), thereby raising ψ_c (Fig. 2). This indirect effect became more apparent during soil drying, as illustrated in Fig. 3 during a hot, dry period starting 9 d after irrigation on DOY 218 (6 August) in 1999. Midafternoon air temperatures rose from 37°C on DOY 227 and 228 (15 and 16 August) to >40°C on DOY 229 to 231 (17 to 19 August) while midafternoon relative humidities declined from 30 to 25% (Fig. 3a). These changes caused simulated and measured midafternoon effluxes of LE to rise from -600 W m⁻² to -650 W m⁻², forcing lower ψ_c in the model to increase root water uptake rates. Midafternoon ψ_c modeled under ambient C_a declined below -1.5 MPa during this 5-d period (Fig. 3b), at which point midafternoon g_c declined markedly (Fig. 3c). Lower LE modeled under elevated C_a allowed midafternoon ψ_c to remain above -1.5 MPa (Fig. 3b) so that midafternoon g_c did not show marked midafternoon declines (Fig. 3c). While ψ_c remained above -1.5 MPa during DOY 227 and 228, LE modeled under ambient C_a exceeded that under elevated C_a , indicated by positive differences in Fig. 3d. When ψ_c declined below -1.5 MPa during DOY 229 to 231, lower midafternoon g_c modeled under ambient vs. elevated C_a (Fig. 3c) reduced midday LE below that under elevated C_a , indicated by negative differences in Fig. 3d. Early morning and late afternoon g_c modeled during this period remained higher under ambient vs. elevated C_a (Fig. 3c) so that LE modeled under ambient C_a remained higher than that under elevated C_a . Similar diurnal differences were detected in measured LE (Fig. 3d), indicating a greater stomatal limitation to energy exchange under ambient vs. elevated C_a as atmospheric and soil water deficits increased. These differences in

Table 2. Statistics from regressions of simulated on measured hourly latent heat fluxes over sorghum under ambient vs. elevated concentrations of atmospheric CO₂ (C_a) in the wet vs. dry treatments during 1998 until frost on 10 November ($n = 1512$ hourly data pairs) and in 1999 until hail on 16 September ($n = 936$ hourly data pairs). Numbers in parentheses indicate C_a and total irrigation during each year.

	b^\dagger	R^2	a	RMSD ‡	RMSE §
	W m ⁻²				
1998					
Ambient (363 $\mu\text{mol mol}^{-1}$)					
Wet (1255 mm)	0.94	0.82	-56	73	85
Dry (476 mm)	0.83	0.85	-54	64	53
Elevated (556 $\mu\text{mol mol}^{-1}$)					
Wet (1255 mm)	0.94	0.82	-57	74	65
Dry (476 mm)	0.91	0.84	-54	64	51
1999					
Ambient (373 $\mu\text{mol mol}^{-1}$)					
Wet (766 mm)	0.92	0.93	-19	57	20
Dry (338 mm)	0.72	0.75	-50	81	62
Elevated (566 $\mu\text{mol mol}^{-1}$)					
Wet (766 mm)	0.90	0.90	-21	66	25
Dry (338 mm)	0.75	0.78	-42	72	103

† From $Y = a + bX$, where Y = simulated flux, X = mean of measured fluxes ($n = 2$), a = intercept (-ve = upward flux), and b = slope.

‡ RMSD, root mean square of differences between simulated and mean measured fluxes.

§ RSME, root mean square of differences between measured replicate fluxes.

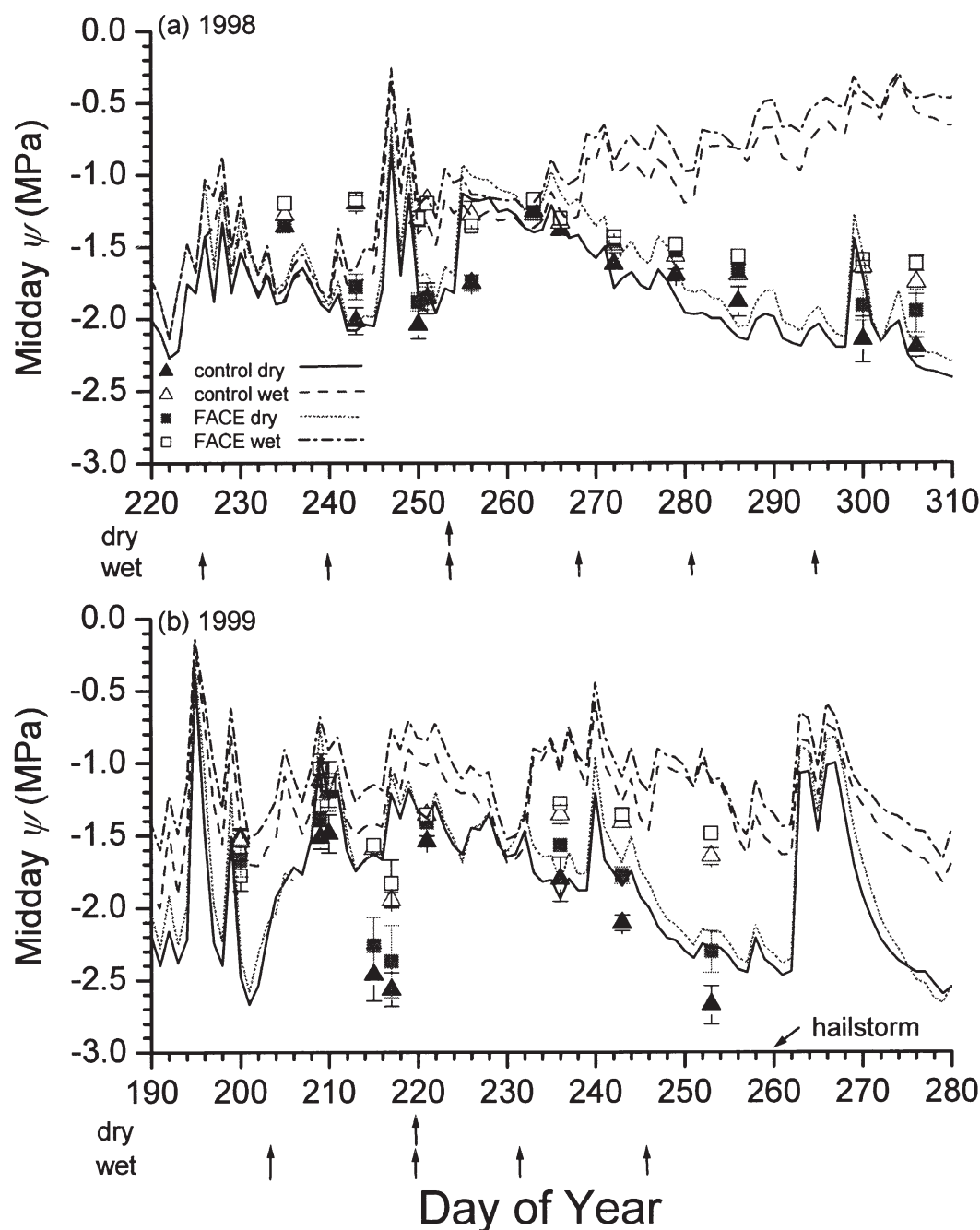


Fig. 2. Midday canopy water potential (ψ_c) simulated (lines) and measured (symbols) in sorghum during the growing seasons of (a) 1998 and (b) 1999 under control wet, free air CO_2 enrichment (FACE) wet, control dry, and FACE dry treatments. Arrows indicate dates of irrigation in wet and dry treatments. For irrigation schedules, see Table 1. Measured data from Wall et al. (2001b).

LE modeled and measured under ambient vs. elevated C_a were more apparent in the dry vs. wet treatment (Fig. 1c and 1d vs. Figure 1a and 1b). Lower midday ψ_c and g_c also reduced midafternoon net CO_2 exchange modeled under ambient vs. elevated C_a during DOY 229 to 231 (Fig. 3e). Thus, gains in CO_2 fixation modeled under elevated vs. ambient C_a depend on both atmospheric and soil water status.

Seasonal Evapotranspiration and Growth under Ambient vs. Elevated Atmospheric Carbon Dioxide

In the wet treatment, lower g_c and hence LE simulated under elevated vs. ambient C_a (Fig. 1b vs. 1a;

Fig. 3d) reduced cumulative simulated (vs. measured) evapotranspiration by 8% (vs. 11%) in 1998 and 5% (vs. 9%) in 1999 (Fig. 4; Table 3). In the dry treatment, higher LE simulated during the onset of water stress under elevated vs. ambient C_a (Fig. 1d vs. 1c) offset lower LE simulated earlier in the growing season so that cumulative evapotranspiration simulated (vs. measured) under elevated vs. ambient C_a was unchanged (vs. unchanged) in 1998 and reduced by only 3% (vs. 6%) in 1999 (Fig. 4; Table 3). Cumulative evapotranspiration in the model was within 10% of that measured by neutron probe in the 1998 and 1999 wet treatments but was about 20% higher and 20% lower in the 1998

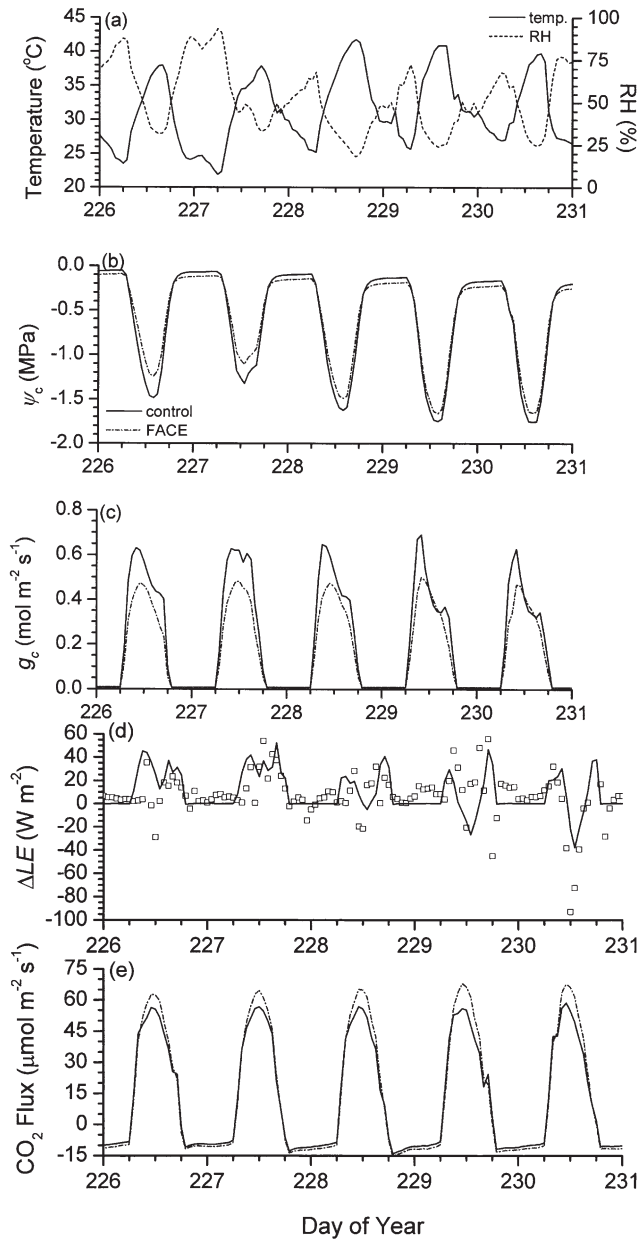


Fig. 3. (a) Air temperature and relative humidity (RH), (b) canopy water potential (ψ_c), (c) canopy conductance (g_c), (d) difference in latent heat (LE) between free air CO₂ enrichment (FACE) and control treatments, and (e) net ecosystem CO₂ flux simulated (lines) and measured (symbols in Fig. 3d) during day of year 227 to 231 (15–19 August) 1999 under control wet and FACE wet treatments. For irrigation schedules, see Table 1.

and 1999 dry treatments, respectively. During 1998, the shallowest neutron probe measurements were taken at 0.46 m, requiring estimates of soil water contents to be made between this depth and the surface (Conley et al., 2001). Agreement between modeled and measured evapotranspiration in the wet treatments during 1998 and 1999 (Fig. 4) was corroborated by agreement between modeled and measured LE ($b > 0.9$, $R^2 > 0.8$ in Table 2). The larger modeled vs. measured evapotranspiration in the 1998 dry treatments (Fig. 4a) was not apparent in the modeled vs. measured LE fluxes ($b < 1$, $R^2 > 0.8$ in Table 2). The smaller modeled vs. measured evapotranspiration in the 1999 dry treatments (Fig. 4b)

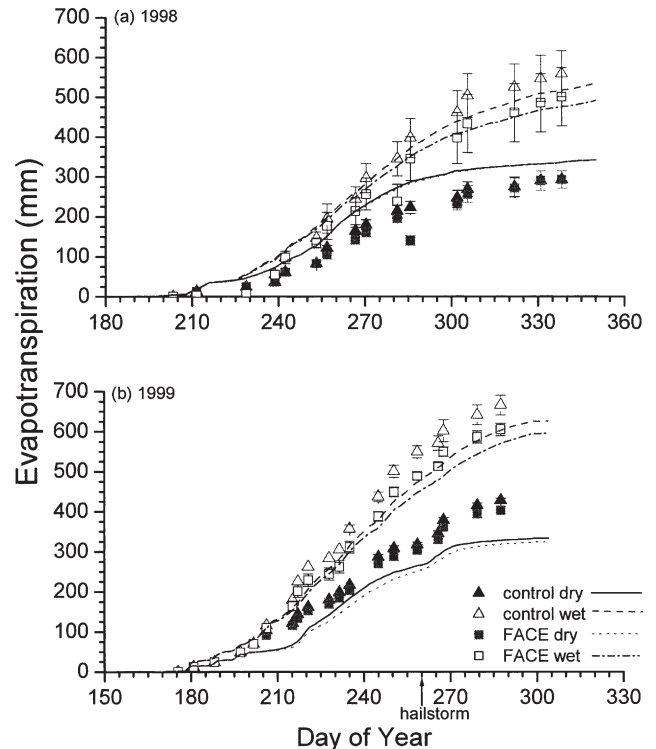


Fig. 4. Cumulative evapotranspiration simulated (lines) and measured (symbols) in sorghum during the growing seasons of (a) 1998 and (b) 1999 under control wet, free air CO₂ enrichment (FACE) wet, control dry, and FACE dry treatments. For irrigation schedules, see Table 1. Measured data from Conley et al. (2001).

was consistent with the smaller modeled vs. measured LE ($b < 0.8$). In both years, evapotranspiration (Fig. 4) was much less than irrigation (Table 1) even though soil water contents declined during sorghum growth, indicating substantial drainage. In the model, much of this drainage was simulated as rapid, gravity-driven flow through macropores. This drainage was not included in the cumulative ET estimated from the neutron probe measurements and did not contribute to ET in the model.

The direct and indirect effects of elevated C_a on CO₂ fixation rates (Fig. 3e) combined to raise simulated (vs. measured) aboveground phytomass in 1998 by 10% (vs. 7%) in the wet treatment and by 26% (vs. 13%) in the dry treatment (Fig. 5a; Table 3). The effects of elevated C_a on CO₂ fixation rates combined with those on g_c to raise simulated (vs. measured) water use efficiency (WUE) in the wet and dry treatments by 20% (vs. 20%) and 26% (vs. 13%), respectively. The dry treatment reduced simulated (vs. measured) aboveground phytomasses in 1998 to 72% (vs. 76%) and 82% (vs. 80%) of those in the wet treatment under ambient and elevated C_a , respectively (Table 3). These reductions in phytomass were relatively smaller than those in evapotranspiration so that both modeled and measured WUE were larger in the dry vs. wet treatment.

Low harvest indices reported in 1999 (Ottman et al., 2001) indicated that late-season growth was impaired by the hailstorm on 16 September so that late-season phytomass in the model was slightly larger than that in the field (Fig. 5b). Elevated C_a raised modeled (vs.

Table 3. Aboveground phytomass, total evapotranspiration (ET), and seasonal water use efficiency (WUE) of sorghum simulated (S) and measured (M) under ambient vs. elevated concentrations of atmospheric CO₂ (C_a) in the wet vs. dry treatments during 1998 and 1999. Numbers in parentheses indicate C_a and total irrigation during each year.

C _a	Irrigation treatment			
	Wet (1255 mm)		Dry (476 mm)	
	S	M	S	M
1998				
Phytomass				
Ambient (363 μmol mol ⁻¹)	696	699 ± 2	498	529 ± 33
Elevated (556 μmol mol ⁻¹)	764	746 ± 19	627	600 ± 36
Elevated/ambient phytomass	1.10	1.07	1.26	1.13
ET				
Ambient (363 μmol mol ⁻¹)	543	559 ± 58	344	293 ± 22
Elevated (556 μmol mol ⁻¹)	500	498 ± 72	345	292 ± 21
Elevated/ambient ET	0.92	0.89	1.00	1.00
WUE				
Ambient (363 μmol mol ⁻¹)	1.28	1.25 ± 0.14	1.45	1.81 ± 0.25
Elevated (556 μmol mol ⁻¹)	1.53	1.50 ± 0.26	1.82	2.05 ± 0.27
Elevated/ambient WUE	1.20	1.20	1.26	1.13
C _a	Irrigation treatment			
	Wet (766 mm)		Dry (338 mm)	
	S	M	S	M
1999				
Phytomass				
Ambient (373 μmol mol ⁻¹)	689	705 ± 8	444	370 ± 26
Elevated (566 μmol mol ⁻¹)	715	698 ± 24	547	437 ± 31
Elevated/ambient phytomass	1.04	0.99	1.23	1.18
ET				
Ambient (373 μmol mol ⁻¹)	626	664 ± 25	333	429 ± 6
Elevated (566 μmol mol ⁻¹)	595	605 ± 15	324	404 ± 9
Elevated/ambient ET	0.95	0.91	0.97	0.94
WUE				
Ambient (373 μmol mol ⁻¹)	1.10	1.06 ± 0.05	1.33	0.86 ± 0.07
Elevated (576 μmol mol ⁻¹)	1.20	1.15 ± 0.07	1.69	1.08 ± 0.10
Elevated/ambient WUE	1.09	1.08	1.27	1.26

measured) aboveground phytomass in 1999 by 4% (vs. -1%) in the wet treatment and by 23% (vs. 18%) in the dry treatment (Fig. 5b; Table 3). Elevated C_a raised modeled (vs. measured) WUE in 1999 by 9% (vs. 8%) and 27% (vs. 26%) in the wet and dry treatments, respectively. Modeled and measured WUE was lower in 1999 than in 1998 because earlier planting caused growth to occur under higher temperatures and VPD. Modeled WUE was larger in the dry vs. wet treatments in 1998 and 1999 because reductions in phytomass were relatively smaller than those in evapotranspiration. However, measured WUE was smaller in the dry vs. wet treatments in 1999 because phytomass was reduced more than was evapotranspiration. This reduction could have occurred if the hailstorm had damaged the dry treatment more than the wet.

Irrigation vs. Yield under Current and Changed Climate

Because only 152 mm of precipitation was received in 1999, modeled shoot mass rose sharply with irrigation up to 600 mm but rose little thereafter (Fig. 6). Modeled grain mass rose comparatively more with irrigation than did shoot mass so that harvest index rose from 0.25 with no irrigation to 0.40 with full irrigation. In *ecosys*, grain set is determined by postanthesis water and C status, both of which were adversely affected by low irrigation. Modeled root mass rose comparatively less with irrigation than did shoot mass so that shoot/root ratios rose

from 3:1 under no irrigation to 8:1 under full irrigation. In *ecosys*, improved shoot water status allows more rapid oxidation of nonstructural C in the shoot and hence comparatively less translocation of nonstructural C to the roots.

Initial model runs under climate change gave lower shoot and grain yields at high irrigation than did those under current climate because sorghum phenology was accelerated by higher temperatures. To avoid confounding phenology with growth, 2.5 phytomers (following the phenology model in Grant, 1989) were added to the juvenile growth stage of modeled sorghum under changed climate to synchronize growth stages with those under current climate. Climate change raised shoot and grain yields by 6 to 10% across a wide range of irrigation rates (Fig. 6). As under current climate, shoot and grain yields under climate change rose little with irrigation > 600 mm. Model results indicated that high sorghum grain yields (e.g., 325 g C m⁻² = ≈8 Mg ha⁻¹ at 12% moisture content) could be achieved with ≈150 mm or ≈25% less irrigation water if air temperatures were to rise by 3°C and C_a by 50%. This water saving was simulated because the effects of higher C_a on transpiration (Table 3) offset the effects of higher temperature on evapotranspiration.

DISCUSSION

Modeled energy balances and water relations, corroborated by measurements of energy flux (Fig. 1) and

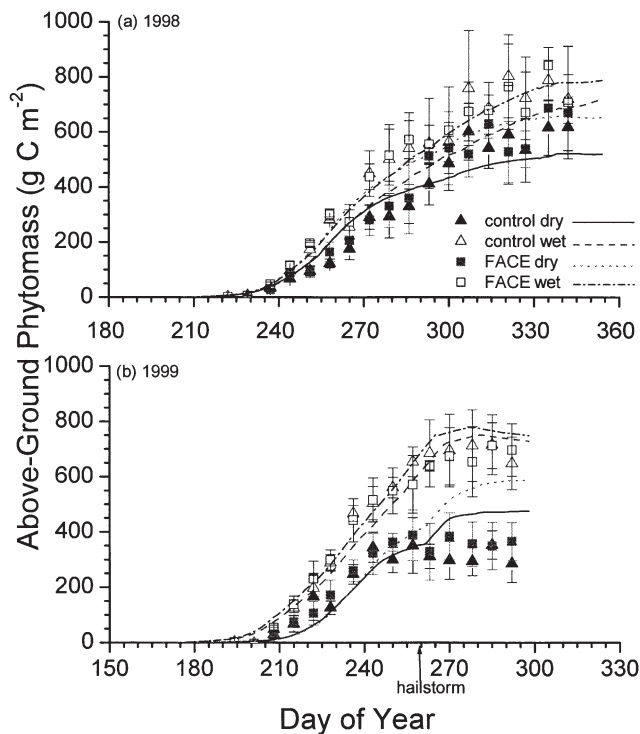


Fig. 5. Aboveground phytomass simulated (lines) and measured (symbols) in sorghum during the growing seasons of (a) 1998 and (b) 1999 under control wet, free air CO₂ enrichment (FACE) wet, control dry, and FACE dry treatments. For irrigation schedules, see Table 1. Measured data from Ottman et al. (2001).

water potential (Fig. 2), indicated that elevated C_a reduced transpiration and hence improved water status of sorghum. These changes lowered the vulnerability of sorghum CO₂ fixation to soil or atmospheric water deficits, even when irrigation was high (Fig. 3e). These observations are consistent with those of Williams et al. (2001), who found that elevated C_a reduced the effects of water deficits on bundle sheath leakiness and C isotope discrimination by reducing transpiration, prolonging soil water availability, and enhancing plant water status. They concluded that direct effects of elevated C_a on CO₂ fixation in sorghum were likely minimal and that indirect effects depended on soil water supply. These model and experimental results support the suggestion by Rogers et al. (1983) that improved WUE (e.g., Table 3) is the most likely cause of the increased sorghum growth frequently reported under elevated C_a (e.g., Amthor et al., 1994). Increases in growth under elevated C_a would therefore be greatest when soil and atmospheric water deficits are most frequent, as indicated by the larger gain in phytomass in the dry vs. wet treatment (Table 3). These gains would likely be smaller in cooler, more humid climates than that at the FACE site in Arizona.

Rising air temperatures hypothesized in projections of future climate will cause greater atmospheric water deficits if assumptions that atmospheric relative humidity remains largely unchanged are correct. Rising C_a should reduce the impact of these deficits on sorghum CO₂ fixation and thereby improve sorghum growth more under future climates than inferred from experi-

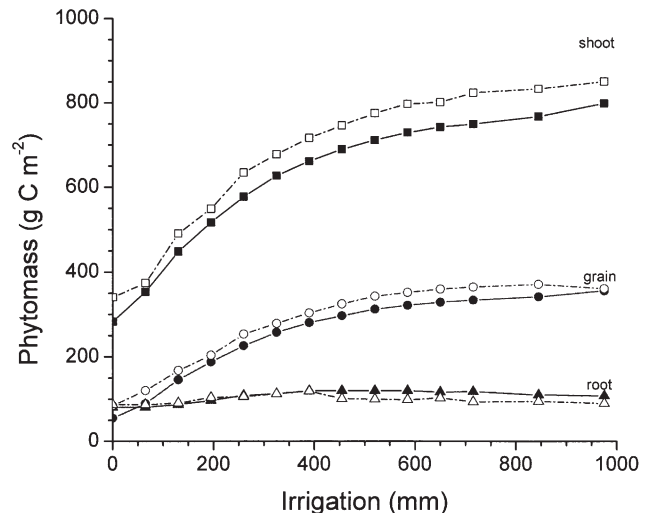


Fig. 6. Response of phytomass to seasonal irrigation amounts (sum of biweekly applications) simulated under current (1999) climate (closed symbols) and under changed (1999 + 3°C, $C_a \times 1.5$) climate (open symbols).

ments conducted under current climate. Model projections of sorghum growth and irrigation requirements under hypothesized climate changes should therefore be based on a robust and accurate simulation of sorghum water relations as affected by C_a . These effects are strongly influenced by diurnal changes in atmospheric conditions (Fig. 3) and so need to be modeled at time steps appropriate to those changes (e.g., hourly). Experiments that monitor diurnal changes in water relations (energy fluxes, water potentials, and g_c 's) provide the best-constrained tests for such models.

The reduction in irrigation requirements of $\approx 25\%$ modeled under higher C_a and temperature (Fig. 6) is consistent with that in Hatch et al. (1999), Strzepek et al. (1999), and Tubiello et al. (2000). The magnitude of the reduction modeled here depended on some critical assumptions: (1) relative humidity and wind speed did not change, (2) precipitation did not change, and (3) the duration of the crop life cycle did not change. Assumption 1 is commonly made due to the large uncertainty in estimating changes in humidity and wind speed. The low precipitation at the FACE site limits the effect of Assumption 2 on irrigation requirements. However most $2 \times C_a$ climate scenarios predict rises in precipitation of $\approx 10\%$ that contribute to modeled reductions in irrigation requirements (e.g., Hatch et al., 1999). Assumption 3 required the addition of 2.5 phytomers to the sorghum life cycle to remove the effects of temperature on the dates of crop growth stages. Climate change is frequently predicted to reduce crop growth and irrigation requirements by hastening crop maturation (Hatch et al., 1999; Strzepek et al., 1999; Tubiello et al., 2000). Lengthening the crop growth cycle by earlier planting under climate change has been predicted to increase the irrigation needed to maintain current sorghum yields (Tubiello et al., 2000). However, such an increase was not modeled under the conditions of this study.

The simulated response of sorghum growth to irrigation, and the impact of climate change on this response

(Fig. 6), should be seen as specific to the site conditions (e.g., weather, antecedent soil water content, soil hydraulic properties, irrigation technique, and fertilization rate) of this experiment. Models such as *ecosys* provide a means to simulate these responses under more diverse site conditions and management practices as needed for regional estimates of water requirements. However detailed, well-constrained tests of these models under well documented site conditions are a vital prerequisite for these simulations.

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REFERENCES

- Acevedo, E., E. Fereres, T.C. Hsiao, and D.W. Henderson. 1979. Diurnal growth trends, water potential and osmotic adjustment of maize and sorghum leaves in the field. *Plant Physiol.* 64:476–480.
- Aguirozabal, L.A.N., S. Pellerin, and F. Tardieu. 1993. Carbon nutrition, root branching and elongation: Can the present state of knowledge allow a predictive approach at a whole-plant level? *Environ. Exp. Bot.* 33:121–130.
- Amthor, J.S., R.J. Mitchell, G.B. Runion, H.H. Rogers, S.A. Prior, and C.W. Wood. 1994. Energy content, construction cost and phytomass accumulation of *Glycine max* (L.) Merr. and *Sorghum bicolor* (L.) Moench grown in elevated CO₂ in the field. *New Phytol.* 124:443–450.
- Azevedo, P.V., and S.B. Verma. 1986. Aerodynamic characteristics of grain sorghum. *Agric. For. Meteorol.* 38:193–204.
- Barber, S.A., and J.H. Cushman. 1981. Nitrogen uptake model for agronomic crops. p. 382–409. *In* I.K. Iskander (ed.) *Modeling waste water renovation—land treatment*. Wiley Interscience, New York.
- Berry, J.A., and G.D. Farquhar. 1977. The CO₂ concentrating function of photosynthesis: A biochemical model. p. 119–131. *In* D. Hall, J. Coombs, and T. Goodwin (ed.) *Proc. Int. Congr. on Photosynthesis*, 4th, Reading, UK. Biochem. Soc., London.
- Bowes, G. 1991. Growth at elevated CO₂: Photosynthetic responses mediated through Rubisco. *Plant Cell Environ.* 14:795–806.
- Conley, M.M., B.A. Kimball, T.J. Brooks, P.J. Pinter, Jr., D.J. Hunsaker, G.W. Wall, N.R. Adam, R.L. LaMorte, A.D. Matthias, T.L. Thompson, S.W. Leavitt, M.J. Ottman, A.B. Cousins, and J.M. Triggs. 2001. CO₂ enrichment increases water use efficiency in sorghum. *New Phytol.* 151:407–412.
- Doussan, C., G. Vercambre, and L. Pagès. 1998. Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption—distribution of axial and radial conductances in maize. *Ann. Bot. (London)* 81:225–232.
- Edwards, G., and D. Walker. 1983. C₃, C₄: Mechanisms, and cellular and environmental regulation, of photosynthesis. Univ. of California Press, Berkely, CA.
- Farquhar, G.D., S. von Caemmerer, and J.A. Berry. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149:78–90.
- Furbank, F.T., and M.D. Hatch. 1987. Mechanism of C₄ photosynthesis. The size and composition of the inorganic carbon pool in bundle sheath cells. *Plant Physiol.* 85:958–964.
- Garcia, R.L., S.P. Long, G.W. Wall, C.P. Osborne, B.A. Kimball, G.Y. Nie, P.J. Pinter, Jr., R.L. LaMorte, and F. Wechsung. 1998. Photosynthesis and conductance of spring-wheat leaves: Field response to continuous free-air CO₂ enrichment. *Plant Cell Environ.* 21:659–669.
- Girma, F.S., and D.R. Krieg. 1991. Osmotic adjustment in sorghum: I. Mechanisms of diurnal osmotic potential changes. *Plant Physiol.* 99:577–582.
- Girma, F.S., and D.R. Krieg. 1992. Osmotic adjustment in sorghum: II. Relationship to gas exchange rates. *Plant Physiol.* 99:583–588.
- Grant, R.F. 1989. Simulation of maize phenology. *Agron. J.* 81:451–457.
- Grant, R.F. 1995. Salinity, water use and yield of maize: Testing of the mathematical model *ecosys*. *Plant Soil* 172:309–322.
- Grant, R.F. 1998. Simulation in *ecosys* of root growth response to contrasting soil water and nitrogen. *Ecol. Modell.* 107:237–264.
- Grant, R.F. 2001. A review of the Canadian ecosystem model *ecosys*. p. 175–264. *In* M. Shaffer (ed.) *Modeling carbon and nitrogen dynamics for soil management*. CRC Press, Boca Raton, FL.
- Grant, R.F., and D.D. Baldocchi. 1992. Energy transfer over crop canopies: Simulation and experimental verification. *Agric. For. Meteorol.* 61:129–149.
- Grant, R.F., R.L. Garcia, P.J. Pinter, Jr., D. Hunsaker, G.W. Wall, B.A. Kimball, and R.L. LaMorte. 1995a. Interaction between atmospheric CO₂ concentration and water deficit on gas exchange and crop growth: Testing of *ecosys* with data from the Free Air CO₂ Enrichment (FACE) experiment. *Global Change Biol.* 1:443–454.
- Grant, R.F., B.A. Kimball, P.J. Pinter, Jr., G.W. Wall, R.L. Garcia, and R.L. LaMorte. 1995b. CO₂ effects on crop energy balance: Testing *ecosys* with a Free-Air CO₂ Enrichment (FACE) Experiment. *Agron. J.* 87:446–457.
- Grant, R.F., P. Rochette, and R.L. Desjardins. 1993. Energy exchange and water use efficiency of crops in the field: Validation of a simulation model. *Agron. J.* 85:916–928.
- Grant, R.F., G.W. Wall, B.A. Kimball, K.F.A. Frumau, P.J. Pinter, Jr., D.J. Hunsaker, and R.L. Lamorte. 1999. Crop water relations under different CO₂ and irrigation: Testing of *ecosys* with the free air CO₂ enrichment (FACE) experiment. *Agric. For. Meteorol.* 95:27–51.
- Hatch, U., S. Jagtap, J. Jones, and M. Lamb. 1999. Potential effects of climate change on agricultural water use in the southeast U.S. *J. Am. Water Resour. Assoc.* 35:1551–1561.
- Hendrey, G.R. (ed.) 1993. FACE: Free-air CO₂ enrichment for plant research in the field. CRC Press, Boca Raton, FL.
- Huband, N.D.S., and J.L. Monteith. 1986. Radiative surface temperature and energy balance of a wheat canopy. *Boundary-Layer Meteorol.* 36:1–17.
- Jara, J., and C.O. Stockle. 1999. Simulation of water uptake in maize, using different levels of process detail. *Agron. J.* 91:256–265.
- Jones, C.A., and J.R. Kiniry (ed.) 1986. CERES: A simulation model of growth and development. Texas A&M Univ. Press, College Station.
- Jones, J.W., K.J. Boote, S.S. Jagtap, G. Hoogenboom, and G.G. Wilkerson. 1988. SOYGRO v. 5.41: Soybean crop growth simulation model. User's guide. Florida Agric. Exp. Stn. Journal no. 8304. IFAS, Univ. of Florida, Gainesville.
- Kimball, B.A., K. Kobayashi, and M. Bindi. 2002. Responses of agricultural crops to free air CO₂ enrichment. *Adv. Agron.* 77:293–368.
- Kimball, B.A., R.L. LaMorte, P.J. Pinter, Jr., G.W. Wall, D.J. Hunsaker, F.J. Adamsen, S.W. Leavitt, T.L. Thompson, A.D. Matthias, and T.J. Brooks. 1999. Free-air CO₂ enrichment (FACE) and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resour. Res.* 35:1179–1190.
- Klepper, B. 1990. Root growth and water uptake. p. 281–322. *In*

- Irrigation of agricultural crops. Agron. Monogr. 30. ASA, CSSA, and SSSA, Madison, WI.
- Ku, M.S.B., M.R. Schmitt, and G.E. Edwards. 1979. Quantitative determination of RuBP carboxylase-oxygenase protein in leaves of several C₃ and C₄ plants. J. Exp. Bot. 30:89–98.
- Mahrt, L., and M. Ek. 1984. The influence of atmospheric stability on potential evaporation. J. Clim. Appl. Meteorol. 23:222–234.
- Ottman, M.J., B.A. Kimball, P.J. Pinter, Jr., G.W. Wall, R.L. Vanderlip, S.W. Leavitt, R.L. LaMorte, A.D. Matthias, and T.J. Brooks. 2001. Elevated CO₂ increases sorghum biomass under drought conditions. New Phytol. 150:261–273.
- Reid, J.B., and M.G. Huck. 1990. Diurnal variation of crop hydraulic resistance: A new analysis. Agron. J. 82:827–834.
- Rogers, H.H., G.E. Bingham, J.D. Cure, J.M. Smith, and K.A. Surano. 1983. Response of selected plant species to elevated carbon dioxide in the field. J. Environ. Qual. 12:569–574.
- Saliendra, N.Z., and F.C. Meinzer. 1991. Symplast volume, turgor, stomatal conductance, and growth in relation to osmotic and elastic adjustment in droughted sugarcane. J. Exp. Bot. 42:1251–1259.
- Seeman, J.R., M.R. Badger, and J.A. Berry. 1984. Variations in the specific activity of ribulose-1,5-bisphosphate carboxylase between species utilizing differing photosynthetic pathways. Plant Physiol. 74:791–794.
- Stitt, M. 1991. Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14:741–762.
- Stockle, C.O., S. Martin, and G.S. Campbell. 1994. CropSyst, a cropping systems model: Water/nitrogen budgets and crop yield. Agric. Syst. 46:335–359.
- Strzepek, K.M., D.C. Major, C. Rosenzweig, A. Iglesias, D.N. Yates, A. Holt, and D. Hillel. 1999. New methods of modeling water availability for agriculture under climate change: The U.S. Cornbelt. J. Am. Water Resour. Assoc. 35:1639–1655.
- Triggs, J.M., B.A. Kimball, P.J. Pinter, Jr., G.W. Wall, M.M. Conley, T.J. Brooks, R.L. LaMorte, N.R. Adam, M.J. Ottman, A.D. Matthias, S.W. Leavitt, and R.S. Cervený. 2004. Free-air CO₂ enrichment effects on the energy balance and evapotranspiration of sorghum. Agric. For. Meteorol. 124:63–79.
- Tubiello, F.N., M. Donatelli, C. Rosenzweig, and C.O. Stockle. 2000. Effects of climate change and elevated CO₂ on cropping systems: Model predictions at two Italian locations. Eur. J. Agron. 13:179–189.
- Wall, G.W., N.R. Adam, T.J. Brooks, B.A. Kimball, P.J. Pinter, Jr., R.L. LaMorte, F.J. Adamsen, D.J. Hunsaker, G. Wechsung, F. Wechsung, S.W. Leavitt, A.D. Matthias, and A.N. Webber. 2001a. Acclimation response of spring wheat in a free air CO₂ enrichment (FACE) atmosphere with variable soil nitrogen regimes: Net assimilation and stomatal conductance of leaves. Photosynth. Res. 66:79–95.
- Wall, G.W., T.J. Brooks, N.R. Adam, A.B. Cousins, B.A. Kimball, P.J. Pinter, Jr., R.L. LaMorte, J. Triggs, M.J. Ottman, S.W. Leavitt, A.D. Matthias, D.G. Williams, and A.N. Webber. 2001b. Elevated atmospheric CO₂ improved sorghum plant water status by ameliorating the adverse effects of drought. New Phytol. 152:231–248.
- Williams, D.G., V. Gempko, A. Fravolini, S.W. Leavitt, G.W. Wall, B.A. Kimball, P.J. Pinter, Jr., R. LaMorte, and M. Ottman. 2001. Carbon isotope discrimination by *Sorghum bicolor* under CO₂ enrichment and drought. New Phytol. 150:285–293.
- Zur, B., and J.W. Jones. 1981. A model for the water relations, photosynthesis and expansive growth of crops. Water Resour. Res. 17:311–320.